

Behavioural responses to encounter of fishing boats in wandering albatrosses

Author information:

5 Julien Collet: pro@colletj.fr, Centre d'Etudes Biologiques de Chizé, UMR 7372 CNRS – Université La Rochelle, France

Samantha C. Patrick: samantha.patrick@liverpool.ac.uk, University of Liverpool, UK

Henri Weimerskirch: henri.weimerskirch@cebc.cnrs.fr, Centre d'Etudes Biologiques de Chizé, UMR 7372 CNRS – Université La Rochelle, France

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Corresponding author :

Julien Collet, Centre d'Etudes Biologiques de Chizé, 79360 Villiers en Bois, France.
Telephone : 05 49 09 35 57

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Summary

Animals are attracted to human food subsidies worldwide. The behavioural response of individuals to these resources is rarely described in detail, beyond chances of encounters. Seabirds for instance scavenge in large numbers at fishing boats, triggering crucial conservation issues, but how the response to boats vary across encounters is poorly known.

Here we examine the behavioural response of wandering albatrosses (*Diomedea exulans*), equipped with GPS tags, to longline fishing boats operating near their colony for which we had access to Vessel Monitoring System data. We distinguish between encounters (flying within 30km of a boat) and attendance behaviour (sitting on the sea within 3km of a boat), and examine factors affecting each. In particular we test hypotheses that the response to encountered boats should vary with sex and age in this long-lived dimorphic species.

Among the 60% trips that encountered boats at least once, 80% of them contained attendance (but attendance followed only 60% of each single encounter). Birds were more attracted and remained attending longer when boats were hauling lines, despite the measures enforced by this fleet to limit food availability during operations. Sex and age of birds had low influence on the response to boats, except the year when fewer boats came fishing in the area, and younger birds were attending further from boats compared to older birds. Net mass gain of birds were similar across sex and not affected by time spent attending boats.

Our results indicate albatrosses attend extensively this fishery, with no clear advantages, questioning impacts on foraging time budgets. Factors responsible for sex foraging segregation at larger scale seem not to operate at this fleet near the colony, and are not consistent with predictions of Optimal Foraging Theory on potential individual dominance asymmetries. This approach complements studies of large-scale overlap of animals with human subsidies.

Introduction

Animals often are attracted by food sources generated by human activities (Oro et al., 2013). Revealing the processes involved in these interactions can be key to improve the effectiveness of management measures. These food resources have contributed to the growth or maintenance of some populations, but also led to dependency on human activities (Bicknell et al., 2013; Bugoni et al., 2010; Oro et al., 2013). In the case of seabirds scavenging on fishery discards, the poor nutritional value of this food can affect reproductive success (Grémillet et al., 2008, 2016; Tew Kai et al., 2013). Accidental captures (“bycatch”) and collisions also negatively affect population dynamics through increased mortality (Anderson et al., 2011; Weimerskirch et al., 1997). Bycatch is one of the primary causes of population declines for more than 30 seabird species (Croxall et al., 2012). Moreover, these effects on populations or even communities can be complex when there are individual differences in the susceptibility to interact with boats (e.g. Barbraud et al., 2013; Mills and Ryan, 2005; Tuck et al., 2015; Votier et al., 2010, 2004). Understanding which species, populations and/or individuals are more susceptible to interact with fishing boats, and why, is thus of primary concern for populations predictions and management.

Within species there can be important variations in the extent of bird-boat interactions between (Granadeiro et al., 2011) and within populations (e.g. Granadeiro et al., 2011; Votier et al., 2010; Patrick et al., 2015; García-Tarrasón et al., 2015). Individual variations in the extent of interaction can often be explained by individual variation in the overlap of foraging grounds with fishing areas. For instance, the frequent foraging sexual segregation of albatrosses and petrels worldwide can lead to sex-biased bycatch in these species (Bugoni et al., 2011; Weimerskirch et al., 1997). Nevertheless, evidence is accumulating that individuals close to vessels may not always end up scavenging at them (Bodey et al., 2014; Sugishita et al., 2015; Torres et al., 2013a). Understanding why some individuals stop or not at boats may thus be an important but mostly overlooked parameter to account for, in complement to large scale overlap assessment (Bodey et al., 2014; Croxall et al., 2013; Torres et al., 2013b).

In particular, dominance interactions may largely influence individual responses to boats and thus create variation in the risk of interaction between individuals overlapping over the same fleets. Indeed, inter- and intra-species interference competition can be high when dense aggregations occur behind boats (Arcos, 2002, chap. 1; Cherel et al., 1996; Furness et al., 1992; Hudson and Furness, 1989). The assumption that competitive ability could affect attraction and response to boats is recurrent in the literature but has rarely been tested (Arcos et al., 2001; Bugoni et al., 2011; Ryan and Boix-Hinzen, 1999; Weimerskirch et al., 1993). This is probably largely due to the challenges of onboard observation conditions: the limited visual reach impedes the detection of non-attracted birds (Skov and Durinck, 2001), moreover it can be difficult to distinguish and focus on single individuals for long periods of time, let alone identify its sex or age. Yet we could expect from Optimal Foraging Theory (OFT) that sub dominant individuals would be less likely to join an aggregation at a boat when they find one (i.e. fly within attraction distance; Lee et al., 2016). They may also have lower energy yields (González-Solís et al., 2000; Lee et al., 2016) or be relegated further from the actual source of food (i.e. stay further from boats when attending them; Parker and Sutherland, 1986).

Wandering albatrosses (*Diomedea exulans*) are known to widely attend fishing boats (e.g. Ashford et al., 1995; Cherel et al., 1996) where they can dominate agonistic interactions over

smaller-sized species (Weimerskirch et al., 1986). They have suffered heavily from bycatch mortality worldwide (e.g. Nel et al., 2002; Otley et al., 2007; Weimerskirch et al., 1997) but little is known about individual variation in their interaction behaviour with boats. Females are 20% smaller than males on average (Shaffer et al., 2001), and when incubating, they tend to forage north of the colony, while males tend to go south where less fishing fleets operate (Weimerskirch et al., 2014). Competitive exclusion of smaller females by larger males has been suggested to explain these patterns (Weimerskirch et al., 1993, but see Shaffer et al., 2001 for an alternative hypothesis). In addition, reproductive performance vary with the age of individuals in this species (Weimerskirch et al., 2005; Pardo et al., 2013; Froy et al., 2013). It has been suggested that this could be related to changes in foraging areas and/or efficiency when ageing (Lecomte et al., 2010; Patrick and Weimerskirch, 2015; Weimerskirch et al., 2014).

Here we examine the behavioural responses of wandering albatrosses from the Crozet Islands to the longline fishing fleet operating near the colony (7 boats in total). We used GPS-tracking data collected over 3 consecutive breeding seasons on incubating birds of known age and sex, together with GPS positions of boats as recorded for the Vessel Monitoring System (VMS). This fine-scale resolution data allowed us to define encounter events (birds remaining within attraction range of a boat, beyond on-board observation scope) and attendance behaviour (sitting within very close range of a boat), hence to evaluate encounter rates, probability to join an encountered boat compared to simply fly past, and several parameters of attendance behaviour. We investigated first the extent of overlap and attendance of wandering albatrosses with the fishing fleet operating close to the colony, second whether these responses to boats differed between sex, age and/or breeding season, third what could be the consequences of attendance behaviours and their variation for the net mass gain of birds at sea.

Material and Methods

Bird data

The study was carried out on Ile de la Possession (Crozet Archipelago 46°S, 52°E). In total, 160 incubating adult birds were equipped with GPS tags (igotU Mobile Action Technology) in 2011, 2012 and 2013 between mid-January and mid-March.

Birds were caught on their nest and the GPS tags, encased in heat shrink tubing, were attached onto back feathers using adhesive Tesa tape. The total mass of attached devices (<32 g including the final package, 0.3-0.5 % of the bird body mass) was well under the 3% recommended threshold (Phillips et al., 2003). Birds were recaptured on the nest after they left for at least one foraging trip. All GPS tags had a recording frequency of 15 min. In addition, 45 females (18 in 2011, 13 in 2012 and 14 in 2013) and 44 males (20 in 2011, 10 in 2012, 14 in 2013) were weighed during both equipment of logger and recapture. Since birds were not equipped during change-overs, we corrected these mass measurements to take into account rates of mass loss on the nest (Weimerskirch, 1995).

This population has been studied and each individual banded since 1966 (Weimerskirch et al., 1997). For individuals that were not banded as chicks, we estimated their minimum age as the date of first capture plus seven years, the youngest age of first breeding attempts (Weimerskirch et

al., 1997). Sex was determined from a combination of size differences (Shaffer et al., 2001), copulation and plumage observations and/or genetic analyses (Weimerskirch et al., 2005). For 5 individuals we were uncertain of the age (n=3) or sex (n=2) and we removed them from the analyses.

For the remaining individuals, a total of 199 tracks were recorded, but only 194 occurred while at least one boat was present on the Crozet shelf (Table 1).

Vessel data

We used data from VMS (boat GPS locations recorded every 1h) and fishing events (GPS points taken at the start and end of each line setting or hauling), both made available from the Pecheker database hosted at the Museum National d'Histoire Naturelle de Paris (Martin and Pruvost, 2007; Pruvost et al., 2011). Following Collet et al. (2015), we merged VMS data with fishing activity data to recreate trajectories, that were then linearly interpolated to estimate one point every 10 minutes. This 10min resolution means that all bird locations would fall within 5min of a vessel location, while keeping a large proportion of non-interpolated vessel GPS positions (~1/3 to 1/5). All VMS points were categorized either as "transit" or "fishing" according to fishing operations records.

In 2011 and 2012, 7 vessels were active over the study period (though not necessarily all simultaneously; range 0 - 6, Table 1). In 2013 only 4 vessels came, with some periods where there were no active boats over the Crozet area.

This fleet complies with mitigation measures aimed at reducing albatross bycatch. These include setting lines only at night, when albatrosses are much less active; such that most interactions occur when boats are hauling lines (see Results).

Behavioural modelling of the bird's response to boats

For each bird location, we determined simultaneous locations (+/- 5min) of each boat present and hence calculated the distance to each of the boats.

When this distance was less than 30km, we considered the bird location within "attraction range", that is, close enough to potentially detect and approach the boat. Indeed data shows that wandering albatrosses display flight movement directed towards boats more than expected by chance up to c.a. 30km, coinciding with the theoretical visual scope limit (Collet et al., 2015).

If the location was within 3km, and with a speed < 10km/h (indicative of a bird sitting on the water), the location was considered as "attending behaviour", with possible feeding attempts (albatrosses need to sit on the water to feed). Note that attendance behaviour is necessarily within attraction range. This 3km value was chosen because wandering albatrosses were shown to sit on the water more than usual at distances up to 3km from boats (Collet et al., 2015).

We defined an "encounter event" as a distinct series of consecutive locations that remains within attraction range (30km) of at least one boat, without exiting this range for more than 4 consecutive GPS locations (c.a. 1h, "time-to return" parameter). Encounter events are defined independently of whether they contain attendance behaviour (fig.1). This in turn enables us to model the behavioural response of birds to boats within the conceptual framework of OFT, considering the boat as a patch. The 1h "time-to-return" value (i.e. allowing an exit of less than only 4 GPS locations) was chosen to limit assumptions on how long albatrosses can remember where previously encountered boats were, once having lost sight of them, while in the same time accounting for

potential inaccuracies in bird-boat distances due to relatively low GPS acquisition frequency (at least one “true” boat position is recorded every hour).

Note that our choices for the attraction threshold and the time-to-return value limit “false negative” detections of encounter events, at the expense of potentially increasing false positive (i.e. no actual boat detection by the bird) or artificially splitting “true encounters”. We include a sensitivity analysis for these two parameters (15-30km, 0.5-24h) in SI1 that shows our conclusions are very robust to this choice.

From this decomposition we could first calculate encounter rates of birds with boats. Then we assessed the proportion of encounter events that did contain attendance behaviour. Assuming that other birds are already attending this boat when our tracked individual makes a decision whether to attend the boat (large number of seabirds indeed attend this fleet; Cherel et al., 1996), this probability to attend a boat is analogous to a scrounging probability within the producer-scrounger framework (Lee et al., 2016). Finally, for each encounter event containing attendance behaviour, we could also determine how much time birds spent in attendance behaviour (calculated either in absolute value or relative to the whole encounter event duration), analogous to a residence time; and how close to vessels they were on average when doing so (assuming more food is available closer to vessels; Collet et al., 2015).

Because wandering albatrosses are less active at night and their visual range is considerably limited at night or when they sit on the sea surface, we only considered in our analyses the 70.5% of encounter events that contained at least one position with speed >10km/h (i.e. “flying”) during daylight (day was defined by a solar elevation higher than 6° below the horizon). These retained encounter events included 93.5% of all locations classified as “attendance behaviour”.

Statistical modelling of the factors influencing the behavioural response

We built 5 independent GLMMs: one for encounter rate (number of encounters offset by trip duration, modelled with a Negative Binomial error structure), one for attendance probability at an encounter (binary response: attendance or not, modelled with a Binomial error structure), and one for each of the parameters describing attendance behaviour, average distance from boat (Gaussian error structure), duration (as the number of attending GPS locations in each encounter, modelled with a Negative Binomial error structure) and proportion of the encounter event spent attending (number of attending GPS locs offset by encounter duration, modelled with a Negative Binomial error structure). Response variables dealing with duration were accounted for by the relevant discrete number of GPS locations instead of absolute time value, because the distributions were largely 0-skewed and more accurately modelled through Poisson-like distributions than Gaussian distributions. We used Negative binomial distributions to account for important over-dispersion (Zuur, 2009).

Age and sex, and their interaction, was included in all of models. To account for large-scale boat density effects, we included the concurrent average number of boats over the Crozet shelf during the bird trip in the encounter rate model. However for all other models, we rather included year and the year-sex and year-age interactions, grouping 2011 and 2012 together against 2013, as there was consistently much less boats in the area in 2013 (in figures we illustrate each year separately). Including year rather than actual concurrent boat density seemed more relevant to us for models of behavioural decisions, as we don’t see how individuals could have accurate information

on the concurrent boat density, but they could have gathered some on the current year conditions, from past trips experience. In addition, for all models except that of encounter rates, we included as a covariate the average number of vessels present within 30km of the bird during the encounter (indeed in 11.0% of encounters more than one boat at a time was within detection range). For all models except that of encounter rates, we also included a variable accounting for vessel fishing activity, and two different variables were calculated, one for attendance probability, and one for attendance behaviour parameters (see below).

Sample sizes are given in Table 2. Random effects fitted were both trip ID and bird ID for all models except that of encounter rates, which is calculated at the trip level hence only included Bird ID. First order interaction terms were removed from models when non-significant, but all fixed (and random) effects were maintained in final models.

Accounting for vessel fishing activity

In the case of the attendance probability at an encounter, it is the minimum time elapsed between the start of the encounter event (when the bird enters the 30km circle) and either the end of the last fishing operations or the start of the next fishing operations (a fishing operation is either line setting or line hauling). This variable will be 0 if the vessel is fishing when the bird enters within 30km of the boat, but could be for instance 30min if the vessel stopped fishing half an hour before the encounter, or started fishing half an hour after the start of the encounter (Fig. 3). This measure allows us to directly compare encounters with or without attendance behaviour.

For all three models of attendance behaviour, we accounted for the vessel activity by including the proportion of the encounter event with the vessel being in active fishing operations.

Mass gain analyses

We modelled the mass gained at sea (g) in function of Year, Sex and level of attendance to boats (the latter proportional to total trip duration). To test the hypothesis that females would obtain less offal at boats because of competition with larger males, we also included the interaction Sex – level of interaction. Following results from Cornioley et al. (2016), we also included mass at departure as a covariate (using within-sex anomalies in mass at departure to account for size dimorphism). Since we had no repeat measures for individuals, we used a linear model without random effects. Similar results were obtained when looking at mass gain rates (g/day at sea).

All analyses were conducted in the R environment. Codes are provided as supplementary material.

Results

Foraging trips varied extensively in duration or distance travelled (194 trips ranging in duration from 2 to 29 days; see Table 1 for more details). All bird trips passed over the Crozet shelf to either reach oceanic waters, or stay on the shelf edge. Some trips were mainly restricted within this shelf (Fig.2A-B), but most contained oceanic portions, to variable extents (average 40% of time over the shelf; see Table 1, Fig.2A-B). Females tended to have longer trips in our sample but the difference was not significant ($t=-1.560$, $p=0.12$), they spent proportionally less time over the shelf ($-20.0 \pm 5.3\%$, $t=3.790$, $df=172$, $p<0.001$; Table 1), but didn't spend less time attending boats ($z=-0.10$, $p=0.99$; Table

1). Boat activity was restricted to the Crozet shelf edge, with boats transiting between different areas within it (Fig. 2C).

Encounter rate and probability to attend boats at encounters

60.3% of the 194 bird foraging trips passed at least once within 30km of a boat during daytime (i.e. ≥ 1 “encounter event”). Attendance behaviour (sitting within 3km of a boat) occurred in only 60.5% of encounter events (236 out of 390), but because trips could contain several encounters, attendance behaviour eventually occurred in 79.5% of these trips with at least one encounter (Table 1). Attendance behaviour represented $7.6 \pm 0.7\%$ of total trip duration on average (max 24.5%; Table 1) for birds attending at least once a boat.

Only the average number of boats present in the Crozet sector during the trip had a significant, positive effect on encounter rate ($z=6.231$, $p<0.001$; Table 2). Females and males had similar encounter rates (Table 2), and they attended boats over the same areas within the shelf (Fig.2C).

Age, sex and year had no influence on the probability to attend after encounter (Table 2) but birds encountering transiting boats were less likely to attend boats than those encountering boats in fishing operation ($z=-2.580$, $p<0.001$; Table 2, Fig. 3). Birds were more likely to be attracted when several boats were within detection range (3.62 ± 1.29 , $z=2.807$, $p<0.01$).

Behaviour while attending boats

The higher the fishing activity of the vessel during an encounter event, the longer in absolute time ($z=12.43$, $p<0.001$) or proportional time ($z=2.828$, $p<0.01$) birds spent attending it (Table 2). Birds attended at closer distances from the boat when boats were active ($\chi^2=8.800$, $df=1$, $p<0.01$; Table 2). The more boats within 30km, the more time remaining attending a boat at an encounter (0.80 ± 0.25 , $z=3.188$, $p=0.001$), but it had no effect on the average distance from boats when attending ($\chi^2=0.157$, $df=1$, $p=0.69$), and there was a tendency to spend a lower proportion of the event attending (-0.32 ± 0.17 , $z=-1.858$, $p=0.06$) when more boats were present.

Hence at the population level, attendance behaviour occurred mainly when boats were hauling lines (66.3% of all attending locations, day or night) or when no fishing operations were ongoing (31.5%) but rarely during line setting (2.1%). As a comparison, 56.3% of non-attending locations that were within 30km of a boat occurred while no fishing operations were ongoing, 34.0% occurred during line hauling, and 9.6% during line setting.

Compared to males, females spent more time attending boats at each encounter event both in absolute value ($z=-2.921$, $p<0.01$; Table 2) and in proportion to the encounter duration ($z=-2.140$, $p=0.03$), although the differences appear rather small (Fig.4A&B). Females were not farther from boats when attending them (Fig. 4C, Table 2).

Fewer vessels were active in 2013 compared to 2011 and 2012 (Table 1). In 2013 birds stayed the same absolute amount of time attending boats during each encounter as in other years (Table 2, Fig. 5a). However they spent proportionally more time out of the “attending area” during an encounter ($z=-2.372$, $p=0.02$; Fig. 5b), and on average stayed further from vessels when attending them ($+656 \pm 204\text{m}$; Fig.5c).

Age had no effect on the attendance behaviour (Table 2), except in 2013 when younger birds were further from boats when attending them, compared to older birds ($\chi^2=5.815$, $df=1$, $p=0.02$, Fig. 5c).

Mass gained at sea

- 5 Birds with comparatively lower mass at departures (accounting for sex dimorphism) had higher absolute mass gains ($t=-5.821$, $df=85$, $p<0.001$).

Whether birds attended boats or not during their trip had no effects on their mass gain ($t=0.886$, $df=85$, $p=0.38$; Fig.6A) without interaction with sex ($t=0.858$, $df=84$, $p=0.39$, Fig.6A). Actually males and females did not differ in mass gained at sea ($t=-1.091$, $df=85$, $p=0.28$). Mass gains were
10 similar across years ($t<0.601$, $df=85$, $p>0.55$).

When examining birds attending boats, the proportion of the total trip duration spent attending boats did not influence the mass gained at sea ($t=0.162$, $df=52$, $p=0.87$; Fig.6B). Again, there were no sex effects ($t=-0.475$, $df=52$, $p=0.64$, Fig.6B), nor interaction between sex and time spent attending boats ($t=0.370$, $df=51$, $p=0.71$), and no differences between years ($t<0.901$, $df=52$,
15 $p>0.37$).

Discussion

Our study is the first to decompose the behavioural response of seabirds to boats into encounter probability, attraction probability after encounter, and attendance behaviour once at boats; and to
20 relate each of these steps to boat activity or individual characteristics. Our results show that 60% of individuals of any age or sex encountered one or more boat, and 80% of them attended at least one of the boat encountered. Hence overall nearly 50% of the birds tracked attended fishing vessels in the Crozet sector, and this number would have been much higher were it not a peculiar year of low boat presence (2013) that limited encounter rates. These results provide support for using individual
25 large scale foraging range overlap with boats as a reasonable proxy for interaction risks in this species (Croxall et al., 2013; Jiménez et al., 2015). Nevertheless, we add on growing evidence that a significant proportion of encounters (~60% here) are not immediately followed by interactions (Bodey et al., 2014; Sugishita et al., 2015; Torres et al., 2013a), suggesting that caution is required to derive precise quantitative prediction of interaction risk from mere overlap data (Croxall et al., 2013;
30 Torres et al., 2013a, 2013b).

Potential dominance effects mediated by sexual size dimorphism or age had a limited influence on behavioural response to boats. In particular the sex or age foraging segregations observed at larger spatial scales in this species (Weimerskirch et al., 2014) did not operate at the scale of fleet attendance, with the exception of younger birds relegated further from boats in 2013
35 when less vessels were present overall (see below). The modelling approach developed here allows the examination of behavioural decisions of animals exploiting human-generated resources using the predictions of Optimal Foraging Theory. OFT predicts that foraging decisions (when to join a patch, how long to exploit a patch, how to distribute among and/or within patch) will differ with individual dominance (e.g. Lee et al., 2016; Parker and Sutherland, 1986). The strong size dimorphism between
40 sexes in this species (Shaffer et al., 2001) is often assumed to lead to such sexual dominance asymmetry (González-Solís et al., 2000; Ryan and Boix-Hinzen, 1999; Weimerskirch et al., 1993) and

thus to different behavioural responses to boats and/or sexual segregation at boats, as is observed at larger scale (Table 1 ; Weimerskirch et al., 1993, 2014). Our results show the opposite: females and males attended boats in the same areas, they had similar encounter rates with boats, had the same probability to join a boat at an encounter. Females spent slightly higher amounts of time attending boats at each encounter than males, and were not relegated further from boats when attending them. Hence, we found no evidence for competitive exclusion by larger males at boats. As a matter of fact, overall, females spent more time attending this fleet during their trip in terms of absolute time. Finally males and females had similar mass gain, which was not influenced by the time spent attending boats. To our knowledge, the size-mediated competitive exclusion hypothesis has been reliably established in only one case for seabirds (González-Solís et al., 2000). The fact that it is not observed in wandering albatross, a highly dimorphic species, questions whether such intra-specific size-dominance plays a significant role in seabird-fisheries interactions, and hence would affect how individuals distribute at boats when they overlap with the same fleets. Further work on other species is nevertheless required as wandering albatrosses both occupy a distinct position in seabird aggregations, where they dominate all other, smaller-sized species (Weimerskirch et al., 1986); and seem to be much less active at feeding aggregations compared to other albatrosses (Ashford et al., 1995; Cherel et al., 1996). Hence the effects of intra-specific dominance may be lower in wandering albatrosses than for other species.

The availability of boats around the island influenced the relationships we found. When boat density was higher, encounter rates were higher. Moreover when there were fewer boats available around the islands in 2013, attending birds were overall further from vessels than in other years, and spent a lower proportion of time attending boats at each encounter (i.e. spent more time off the 3km area while still remaining close to boats). Nevertheless, the absolute value of time spent attending boats at each encounter was similar across years, as was the attraction probability. This might be the result of an increased spatial competition if a similar number of seabirds concentrated around a fewer number of vessels. The 2013 effect on the attendance distance was most marked in younger rather than older birds (Fig.5c), suggesting that experience might play a role on the efficiency of individuals to position within aggregations when bird density increases because of lower boat density. This may be of importance since collisions or bycatch is more likely to occur closer to the boat rather than away when lines are in deeper waters. However we stress that further work is needed to confirm this age pattern.

As sex and age were poor predictors, a large part of the variation in the attendance behaviour remains to be explained. The value of 30km we used for the attraction range may be an upper limit to the visual detection and therefore not always realised (Collet et al., 2015), so that birds may simply not have detected boats in most possible encounters (Weimerskirch et al., 2000). Using more complex modelling approach to try estimating separately detection probability from attraction probability after detection, and including data on wind and/or weather, may be the way forward. The probability to be attracted increased when adopting more restrictive encounter definitions (such as shorter attraction range thresholds), but even then a non-negligible proportion of encounters were not “exploited” by birds (S.I.1).

We nevertheless found that a boat engaged in fishing operations was more likely to attract birds, and that birds stayed attending the boat for longer when these were actively fishing. This is despite the mitigation measures that have been implemented since the mid-2000 in the Crozet exclusive

economic zone to reduce bycatch. These measures include the setting of lines only at night when diurnal albatrosses rest at the sea surface (explaining why attendance occurred mainly during hauling and why we excluded night locations for our analyses), the use of weighted lines for faster sinking speeds (wandering albatrosses are strict surface feeders), and ban of any discarding during fishing operations: fishermen have to delay it to the end of operations, when possible even after a block of several neighbouring lines have been hauled, and to favour non-fishing areas for doing so (J.O. des T.A.A.F. 2010, sec. Annexe II-Exercice de la pêche, and more recent ones).

The presence of government observers on-board each boat ensures that these measures are effectively enforced. Although these measures are extremely efficient to eliminate albatross bycatch by this fleet (approximately null in the past decade; Delord et al., 2005), our results suggest they may not diminish bird attraction to boats. Even more, it questions why birds keep attending boats, especially during fishing operations, while supposedly much less food is available to them. Either they benefit from the presence of sub-surface feeders such as diving petrels (Jiménez et al., 2012) and/or depredating killer and sperm whales (Tixier et al., 2010), that could facilitate access to baits or captures to surface feeders, either a large proportion of the time spent attending boats actually is not food rewarded (Ashford et al., 1995; Cherel et al., 1996). While it seemed not to have impacts on mass gain, such a behavioural trap could affect time budgets and cause issues for chick-rearing birds with higher constraints on time and energy (see also Grémillet et al., 2008, 2016 for impacts of low food quality at boats). The facts that most individuals in our study may have been born before the implementation of these measures, and/or that this species can encounter other fleets further in their range, including during their sabbatical years, may help explain the persistence of this attraction during operations. Yet there is anecdotal evidence that wandering albatrosses can quickly alter their foraging behaviour after a change in food supplies (Gain, 1914 cited by ; Tickell, 2000), and our results indeed support some behavioural flexibility.

Another unknown aspect is how the presence of boats on the Crozet shelf affects wandering albatross foraging behaviour at larger scales (Tew Kai et al., 2013). Fishing activity in the Crozet area started in the late 1990's (Pruvost et al., 2015), and incubating birds from this colony exploited the shelf slope area before the commencement of fisheries, however the extent of this behaviour at this time is unclear (Weimerskirch et al., 1993). We show here that the proportion of time attending this fleet had no effects on the mass gained at sea, and represented on average less than 8% of the time spent at sea, so that individuals from this colony can still largely rely on other food resources. Determining whether the encounter rates are too high to be opportunistic rather than the result of an active searching process is difficult.

To conclude, we show here that wandering albatrosses attended extensively the fishing fleet operating close to the breeding grounds. Individuals of all age and sex had similar encounter rates with this fleet, and attended it in similar proportions, except when resources were scarce and younger birds appeared to be attending further from boats than older birds. Given the strong age and sex patterning found in the foraging behaviour of this species at larger scale, our results suggest that segregation is limited at boats accessible to all individuals, supporting the use of overlap data to assess risks of encounters in this species. Further work is needed to determine whether this applies to other species or fisheries, where competition intensity may be different. We identified vessel operations as a factor affecting both attraction probability and time spent attending behind boats, despite enforced measures to reduce boat attractiveness. This may have unforeseen consequences on time budgets if boats act as poorly rewarding foraging cues, and it highlights that mitigation

measures designed for limiting bycatch will probably have a limited impact for the reduction of seabird behavioural dependency on boats when it occurs. Furthermore, we add on growing evidence that a large proportion of encounters are not immediately followed by attending behaviour, calling for caution when trying to derive quantified interaction probabilities from large scale overlap data.

Our results suggest that detection limits rather than bird decision making may be involved in our case, although this will require further investigation. However we stress that when encounter rates are no longer limiting factors (high boat density and/or predictability), the relationship between overlap and interaction levels may be far from linear. Finally, while we developed this approach in the context of seabirds-fisheries interactions, it could be adapted for other human activities attracting wildlife, or to gain fundamental insights into wild animal decision-making and/or detection capabilities.

Acknowledgments

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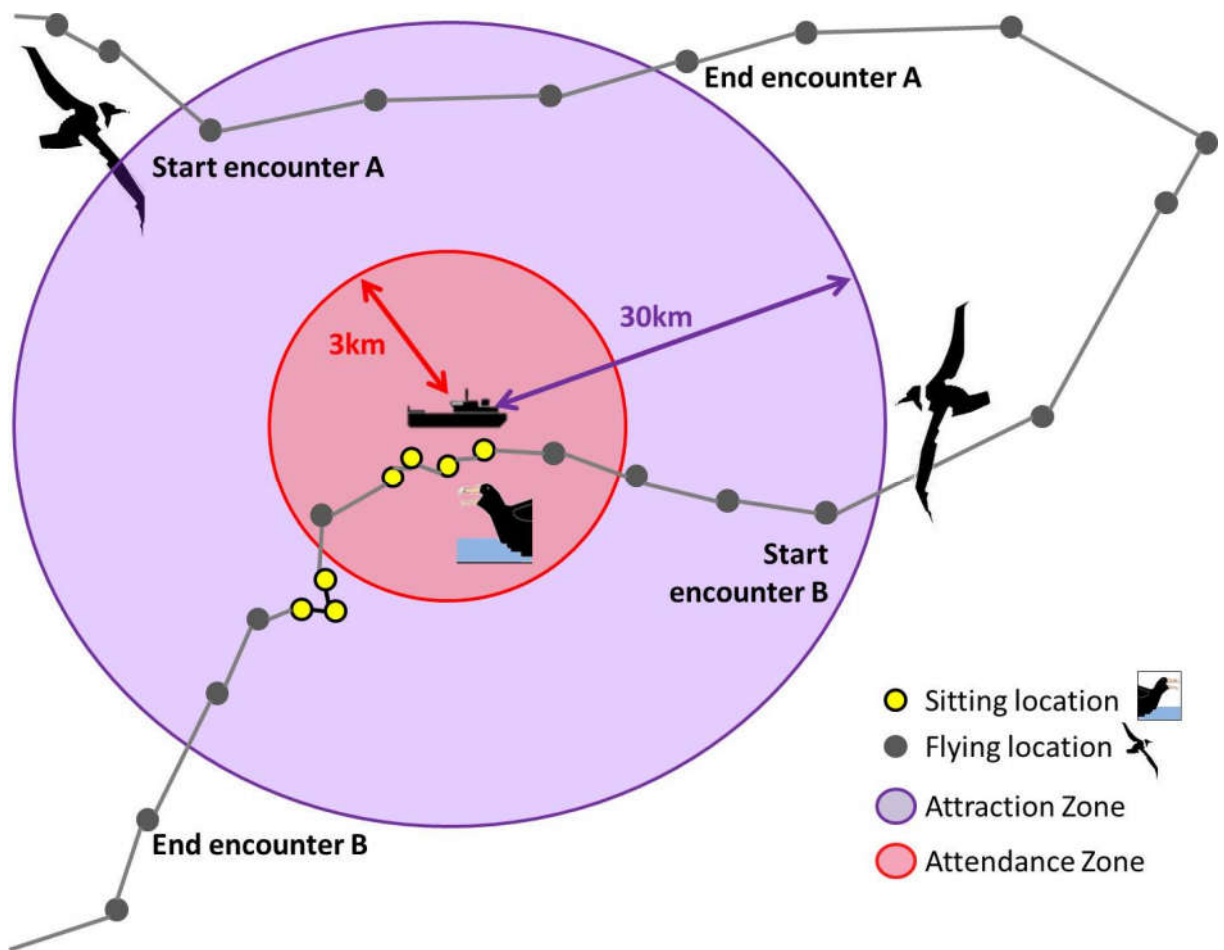


Figure 1: Definitions used for modelling the behavioural response to boats (note that the circles actually move with the boat). Two hypothetical encounter events are depicted, A) Encounter without attendance, lasting 3 locations; B) Encounter followed by attendance, lasting 14 locations including four "attendance behaviour" locations (speed < 10 km/h indicating sitting, in yellow, 29% of the encounter, at an average distance < 3 km). There is a lag of 6 locs in between the two encounters, which is more than our threshold time-to-return value (4 locs) so A and B are considered distinct encounters.

5

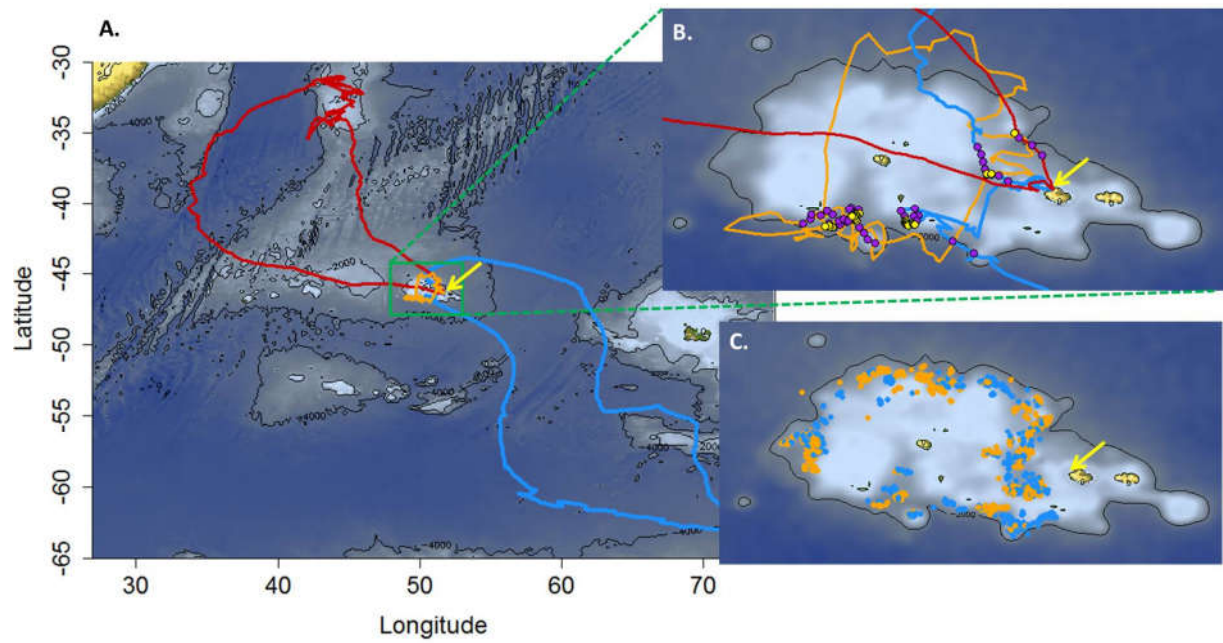


Figure 2: A. Three typical foraging trips of wandering albatrosses from Crozet (yellow arrow). Two mostly oceanic trips, one from a female (in red, 15.5 days), and one from a male (in blue, 19.3 days) and one trip (in orange, from a female, 3.9 days) remaining over the Crozet shelf. B zooms over the Crozet shelf. Locations in flight within 30km of a boat shown in purple, and locations sitting within 3km of a boat ("attendance") shown in yellow. C shows all locations classified as attendance behaviour for males (blue) and females (orange).

5

	Total	Males			Females			Year		
		Total males	26+ years	<26 years	Total females	26+ years	<26 years	2011	2012	2013
Number of tracks (of individuals)	194 (156)	91 (71)	29 (20)	52 (41)	103 (85)	46 (38)	57 (47)	43 (43)	24 (24)	127 (107)
Max Range (km)	1052 ± 56	1000 ± 97	1002 ± 149	998 ± 128	1098 ± 63	1014 ± 95	1165 ± 85	748 ± 102	977 ± 179	1169 ± 69
Total Distance covered (km)	4685 ± 252	4433 ± 399	4418 ± 676	4443 ± 487	4907 ± 319	4409 ± 423	5310 ± 460	3325 ± 406	4537 ± 678	5173 ± 328
Duration (days)	9.3 ± 0.3	8.7 ± 0.4	8.7 ± 0.7	8.7 ± 0.6	9.8 ± 0.5	10 ± 0.7	9.6 ± 0.7	9.1 ± 0.7	9.2 ± 0.8	9.4 ± 0.4
Average number of boats present during the trip	2.1 ± 0.1	2.2 ± 0.2	2.4 ± 0.3	2.0 ± 0.2	1.9 ± 0.1	2.0 ± 0.2	1.9 ± 0.2	4.0 ± 0.3	2.9 ± 0.0	1.2 ± 0.0
Proportion of trip over Crozet shelf (%)	40.2 ± 2.7	50.7 ± 4.2	53.6 ± 6.6	48.6 ± 5.5	30.9 ± 3.2	32.3 ± 5.2	29.8 ± 4.0	59.1 ± 5.8	42.0 ± 8.2	33.5 ± 3.1
% of trips (# tracks, # individuals) with encounter event	65.3 (117, 106)	84.5 (59, 49)	69.2 (27, 23)	61.5 (32, 28)	56.3 (55, 51)	51.3 (25, 22)	57.9 (33, 29)	66.7 (39, 39)	87.5 (21, 21)	44.9 (57, 49)
% of trips (# tracks, # individuals) attending boats when having the opportunity	77.8 (91, 81)	83.1 (49, 49)	82.6 (25, 22)	75.0 (24, 18)	72.4 (42, 41)	72.7 (18, 17)	77.1 (34, 24)	89.7 (36, 35)	66.7 (14, 14)	73.7 (42, 37)
Absolute time spent attending boats (hours) during a trip, when >0	11.0 ± 1.0	9.7 ± 1.1	9.9 ± 1.7	9.5 ± 1.4	12.6 ± 1.6	15.3 ± 2.7	10.5 ± 2.0	12.5 ± 1.6	8.8 ± 2.4	10.5 ± 1.4
Proportion of trip spent attending boats (%) when >0	7.6 ± 0.7	7.5 ± 0.8	8.1 ± 1.4	6.9 ± 0.9	7.7 ± 1.1	9.0 ± 1.6	6.7 ± 1.5	8.1 ± 1.1	6.1 ± 1.8	7.7 ± 1.0

Table 1 : Trip-level statistics in relation to year, age and sex. Note that age was treated as a continuous variable in all analyses. Statistics are means ± s.e. over all concerned trips, except for coloured lines giving percentages.

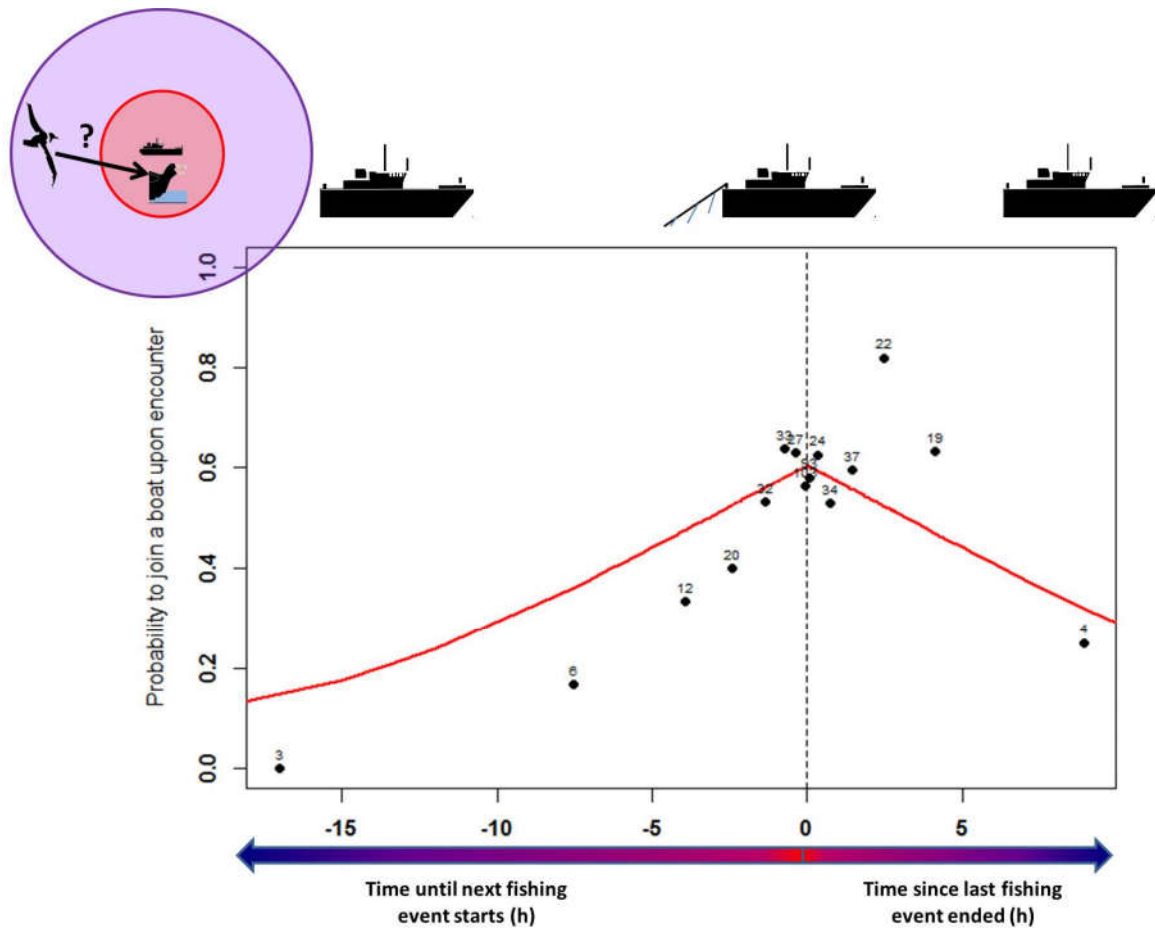
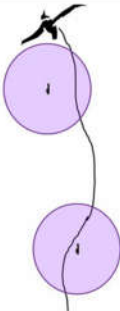
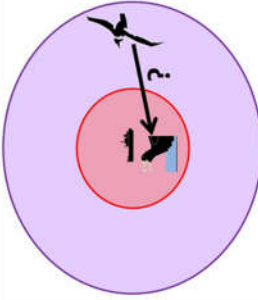
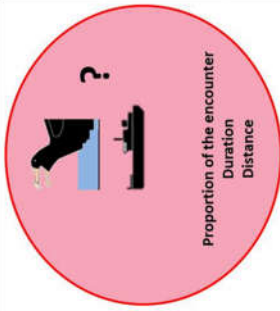


Figure 3: Observed (filled dots) and modelled (red solid line) probability to attend a boat upon encounter, depending on time to closest fishing activity at the start of the encounter. Numbers of observations over which proportions were calculated are indicated above each dot. Dashed line shows when the boat was active at the start of the encounter.

Table 2 : Model outputs for the behavioural responses to boats. Effects of the number of boats present within 30km are indicated in the Results and not reported here. Estimate +/- s.e. are given when they were significant, with the color of the cell indicating significance level (black: $p < 0.001$, dark grey: $p < 0.01$, grey: $p < 0.05$, light grey: $p < 0.10$, lighter grey $p > 0.10$). N.S. for non-significant.

		Description		Influencing factors (estimators ± standard errors)							
	Model	Population average value	N (encounters, tracks, individuals)	Average number of boats	Boat activity	Age	Sex (F vs M)	Age:Sex	Year 2013	Year:Age	Year:Sex
	Encounter rate	0.30 ± 0.03 per day of trip	*,194, 156	+0.45 ± 0.04		NS	NS	NS			
	Probability to interact at an encounter	60.5%	390, 117, 100		+0.19 ± 0.07	NS	NS	NS	NS	NS	NS
	Time spent attending boat per encounter	4.34 ± 0.29h	236, 91, 81		+2.17 ± 0.33	NS	+0.39 ± 0.13	NS	NS	NS	NS
	Proportion of the encounter spent attending boats	28.8 ± 1.0%	236, 91, 81		+0.67 ± 0.24	NS	+0.21 ± 0.10	NS	-0.19 ± 0.09	NS	NS
	Average distance from boats when attending them, per encounter	1254 ± 34m	236, 91, 81		-569 ± 192	+5.88 ± 5.43	NS	NS	+656 ± 204	-18.88 ± 7.92	NS
											

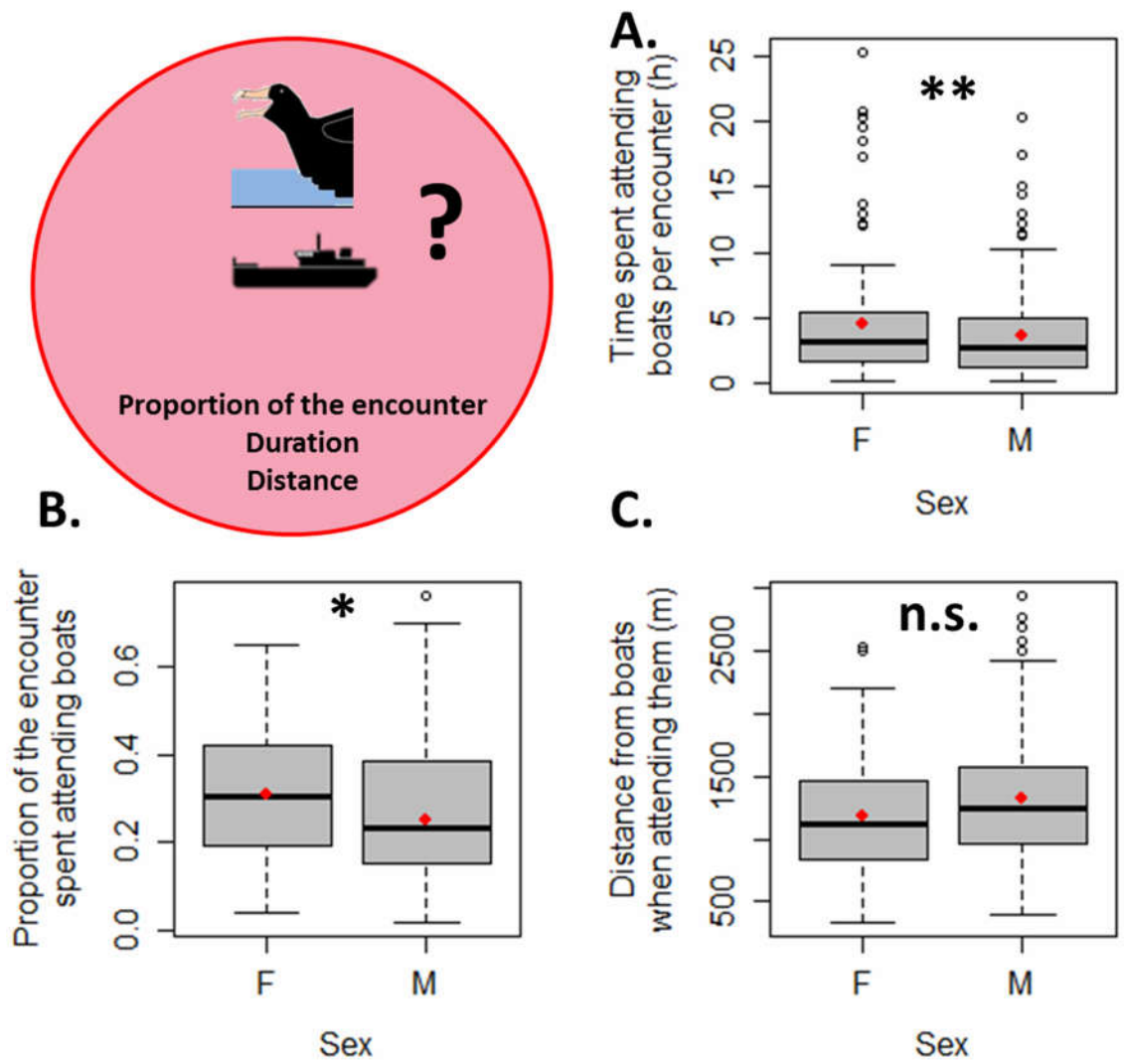


Figure 4: Sex effects on attendance behaviour: duration (a), proportion of the whole encounter event (b) and average distance from boats (c). Modelled means (Table 2) are shown as red dots.

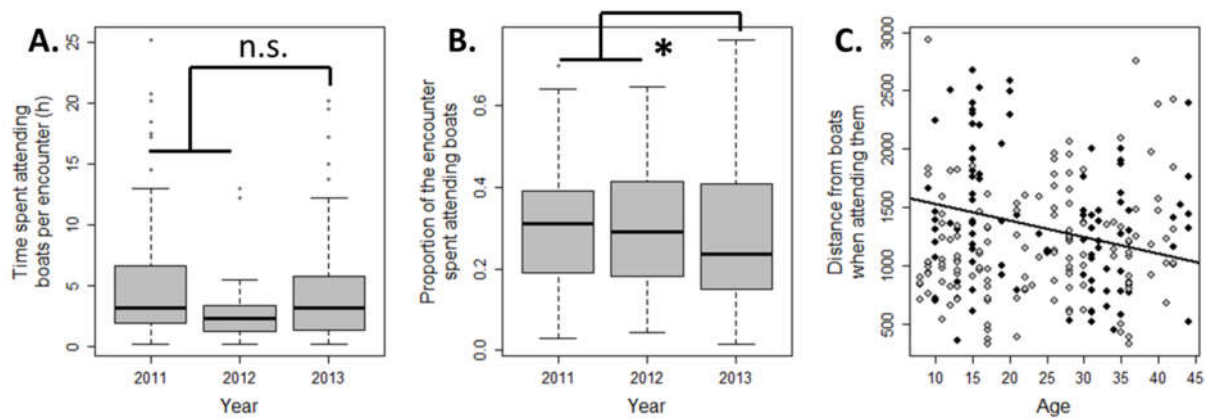


Figure 5: Year effects on attendance behaviour: duration (a), proportion of the whole encounter events (b) and distance from boats (c). The year effect depended on the age of birds in 2013 (black dots, regression line drawn) but not in 2011-2012 (grey dots).

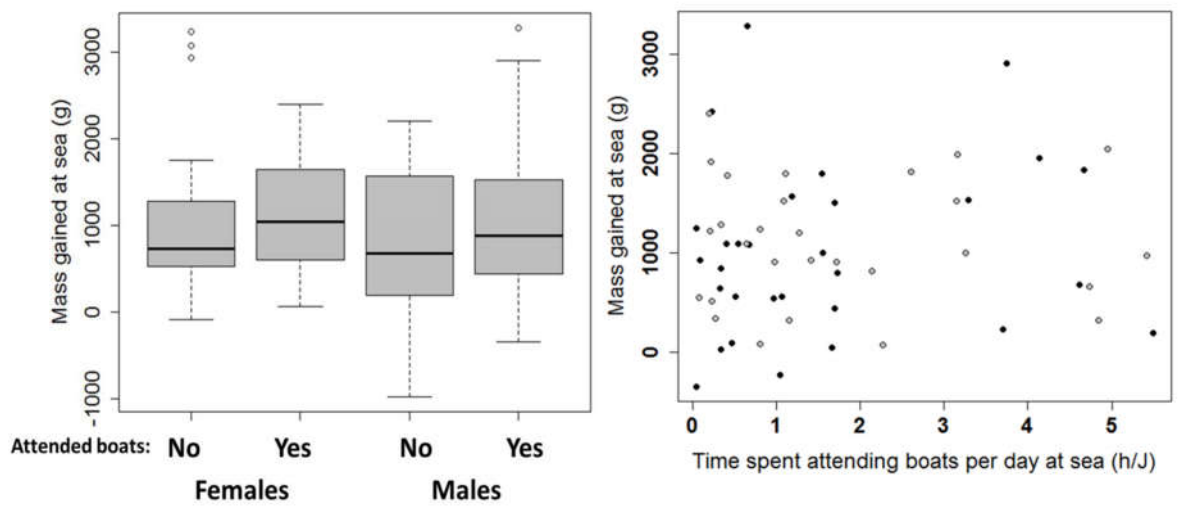


Figure 6: Net mass gained at sea by males (in black in B) and females (grey in B), whether or not they attend boats (A), and for those which did attend boats, in function of the proportion of their time at sea spent attending boats (B).